THE PROBLEMATIC PERMIAN REPTILE
EUNOTOSAURUS

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CONTENTS

SYNOPSIS

Eunotosaurus, which has been suggested as a possible ancestral chelonian, is re-investigated and described. Little of the skull is preserved. The vertebrae are amphicoelous and notochordal, with small neural spines and horizontal zygapophyses. There are small intercentra. Ten dorsal vertebrae are known. The outer surfaces of the dorsal ribs are greatly expanded antero-posteriorly. There is a single sacral attachment. There is no trace of dermal ossifications, and it seems likely that the expanded ribs themselves had a protective function and were covered by horny scales. The body is short and not very flexible. The humerus is rather slender, with the ends expanded and at an angle of *c.* 50° to one another; there are entepicondylar and ectepicondylar foramina.

The structure of its vertebrae indicates that *Eunotosaurus* is a cotylosaur, but it shows no close similarities to any other member of that group and is therefore best regarded as constituting a separate family of the sub-order Captorhinomorpha. The absence of separate ribs on the last dorsal vertebra may preclude *Eunotosaurus* from being ancestral to the Chelonia. Its carapace-like form, shortened body and elongate dorsal vertebrae appear to be merely convergent with the chelonian structure, and there are no other features suggesting relationship between the groups.

I. INTRODUCTION

THE first specimen of *Eunotosaurus africanus* was described and named by Seeley in 1892, who noted also that the slender elongate vertebrae, which lack transverse processes, were reminiscent of those of the Chelonia, and that the expanded ribs " simulate the ribs and costal plates of chelonians " (1892, p. 585). These suggestions were later expanded by Watson (1914) who deduced, from the characters and trends of later chelonians, the structure of an ancestral " Archichelone ". After studying the four specimens of *Eunotosaurus* in the British Museum (Natural History) and finding structures which he identified as dermal ossifications, Watson compared *Eunotosaurus* with his hypothetical " Archichelone ". He concluded that " it is by no means improbable that it is an actual ancestor of the Chelonia " (1914, p. 1020).

Thenceforward, *Eunotosaurus* was often placed in a separate sub-group of the Chelonia (e.g. Nopcsa 1923; Romer 1966). Apart from passing references by Broom (1941) and Gregory (1946), no further study was made of *Eunotosaurus* for nearly fifty years. The next re-appraisal was that of Parsons & Williams (1961), who concluded

that the expanded ribs and possible dermal ossifications were basically quite unlike the chelonian carapace and are " primarily interesting as *another* method by which a similar result may be achieved " (1961, p. 98).

This denial of its affinities with the Chelonia left the taxonomic position of *Eunotosaurus* completely uncertain, since no other relationship for the genus had ever been suggested. Together with the greater potentialities of the newer chemical and mechanical techniques of preparation, this made it seem worthwhile to attempt a re-study of the genus. Thanks to the extremely generous co-operation of the authorities of the British Museum (Natural History), the U.S. National Museum in Washington, the Bernard Price Institute for Palaeontological Research in Johannesburg, and the South African Museum, Cape Town, all the eleven known specimens of *Eunotosaurus* were made available for study and preparation.

II. SYSTEMATIC DESCRIPTION

MATERIAL AND METHODS. For convenience, each specimen has been allocated a letter by which reference will be made to it in the remainder of this paper. The skeletal elements identified from each specimen are as follows.[1]

Specimen A BM(NH) No. R1968 (Holotype). Figured by Seeley, 1892, figs. 1, 2. Seven articulated vertebrae and their ribs; damaged right pubis (?) and ilium; right femur, proximal ends of right tibia and fibula.

Specimen B BM(NH) No. R4054. Figured by Watson 1914, pl. VII, figs. 3, 4. Eight articulated vertebrae and their ribs, plus a single more anterior rib; impressions of small parts of the right scapula and ilium.

Specimen C BM(NH) No. R4949. Ten articulated vertebrae and their ribs; eroded coracoid region; isolated podial elements.

Specimen D BM(NH) No. 49423. Figured by Watson 1914, pl. VII, figs. 1, 2. Eroded remains of five articulated vertebrae and of their ribs; damaged right half of pectoral girdle, and interclavicle; remnants of both humeri.

Specimen E BM(NH) No. 49424. Reconstruction of skull figured by Watson 1914, text-fig. 1. Eroded snout and lower jaw; seven articulated vertebrae and their ribs; remnants of right scapula and of both humeri; both pubes (?).

Specimen F SAM No. K1132. Eight articulated vertebrae and their ribs, plus three isolated vertebrae; ventral portion of pectoral girdle, proximal part of left humerus.

Specimen G SAM No. K1133. Nine articulated vertebrae and their ribs; traces of left scapula and of right humerus.

Specimen H SAM No. 4328. Natural mould of nine articulated vertebrae and their ribs, of right half of pelvic girdle, and of parts of left femur.

Specimen I BPI No. 3514. Five articulated vertebrae and their ribs, plus other disarticulated, poorly preserved elements including an interclavicle.

[1] Abbreviations:

BM(NH)—British Museum (Natural History), London
SAM—South African Museum, Cape Town
BPI—Bernard Price Institute for Palaeontological Research, Johannesburg
USNM—United States National Museum, Washington D.C.

Specimen J BPI No. 3515. Five articulated vertebrae and their ribs, plus five other displaced vertebrae (including one cervical and one caudal) and a rib; proximal end of left humerus, and two podial elements.

Specimen K USNM No. 23099. Series of three vertebrae and five pairs of ribs, plus four other displaced vertebrae; right humerus, right ilium, damaged left pelvis and right (?) scapula.

As far as is known, all the specimens are derived from the Middle Permian Tapino-cephalus Zone of the Beaufort Series of South Africa. The locality data of specimens C, E, G and H are unknown, except that specimen H was acquired from the museum of the boys' school at the town of Fraserburg Road, in the Cape Province of South Africa. The remaining seven specimens were all found within a radius of 40 miles of that town. Specimens A and D were found on the farm Weltevreden, and specimen B on the farm Rietfontein; these two farms lie in the Prince Albert District, about 15 miles south-west of Fraserburg Road. Specimen F was found on the farm Boes-mansrivier, in the Beaufort West District, about 25 miles north-east of Fraserburg Road. Specimens I, J and K were collected about half a mile east of the Waikraal River on the farm De Bad, which lies in the Beaufort West District about 40 miles north-west of Fraserburg Road. These three specimens were collected in 1961 by Dr. N. Hotton III of the U.S. National Museum, Washington and Mr. James Kitching, Field Officer of the Bernard Price Institute for Palaeontological Research, Johannes-burg, who kindly provided all the above locality data.

The specimens are preserved in a non-calcareous, olive-grey, silty mudstone (sub-greywacke), which shows traces of haematite staining. Most specimens appear to have been fossilized lying on their dorsal or ventral surfaces, so that compression has caused the ribs to lie more or less in the horizontal plane. Specimens B and G, however, appear to have been lying on their side when fossilized; as a result, the ribs have come to lie more in the vertical plane, with the distal ends of the right and left ribs nearly touching. These two specimens therefore look very like bivalve molluscs in shape (see Watson 1914, pl. VII, figs. 3, 4).

Specimens A, C, D, E, I, J and K were prepared with acetic acid until any identifi-able and well-preserved skeletal elements were free of matrix. The shapes of any superficial impressions of bones were conserved by filling them with a hard-setting plastic before starting to prepare the specimen. Specimens B, F and G were not prepared as their matrix did not soften in acetic acid. Specimen H, a natural mould, was studied from rubber latex casts.

Some specimens contain articulated series of ribs and vertebrae. Comparison of these series has made it possible to homologize them; the resulting combined series includes ten presacral vertebrae (numbered 1–10), one sacral vertebra and two caudal vertebrae. Dorsal vertebrae and ribs belonging to such articulated series have there-fore been referred to in the text by a letter identifying the specimen, followed by the appropriate number indicating its position in the dorsal series. Disarticulated ele-ments are preserved in specimens F, I, J and K; these have been numbered 21–40 in each specimen, so as to avoid confusion with elements from the articulated series. Thus " vertebra K5 " indicates the articulated fifth dorsal of specimen K, while " vertebra F27 " indicates a disarticulated element from specimen F.

All paired postcranial bones have been drawn as though they were those of the left side. Where necessary, bones of the right side have therefore been drawn as mirror images of themselves.

OSTEOLOGY. SKULL. The only fragment of the skull, 2 cm. long and up to 1·5 cm. across, is that found in specimen E. Unfortunately it is even less complete than Watson (1914) believed, and includes only the middle region of the snout and lower jaw, lacking both the anterior tip and everything posterior to the level of the transverse processes of the pterygoids. The skull has also been eroded or broken horizontally at the level of the palatal bones, so that all the roofing bones are missing, and the palate is visible dorsally in horizontal section.

Lateral view (Fig. 1A, B; Pl. 1A). Apart from the incomplete and damaged tooth rows and portions of the tooth-bearing bones, very little can be seen. The teeth are simple and rather blunt. The right and left tooth-bearing bones do not meet anteriorly, and those of the left side were slightly dislocated outwards from the palatal bones. On the left side, the portion of bone which bears the three most anterior upper teeth appears to be part of the premaxilla; this suggestion is supported by several features. It is separated, by a very narrow band of matrix, from the more posterior bone, the anterior end of which is smooth, unbroken and toothless, suggesting that this is the anterior end of the maxilla, overlapped by the posterior end of the premaxilla. The fragment of premaxilla is also somewhat inclined antero-ventrally, though this may be a post-mortem occurrence.

Behind the fragment of premaxilla, nine teeth are visible on the preserved portion of the left maxilla. On the right side there is no trace of the premaxilla, and all twelve teeth visible in the upper jaw belong to the maxilla. The more posterior of these teeth are represented only by small fragments and by curved depressions in the underlying matrix.

Most of the lower teeth are obscured by matrix or by the upper teeth. One or two of their tips are visible and bear slight longitudinal grooves and ridges. The lower jaw itself is fairly deep, though thin in cross-section. On the right side, the anterior end of the angular can be seen overlapping the dentary. More posteriorly, the angular forms the ventral margin of the lower jaw, which is here rather wider and flattened. Medially there is a large splenial.

Dorsal view (Fig. 1C; Pl. 1B). The dorsal surface of the palatal bones has been lost, and the bones have also been broken and dislocated. Despite these difficulties, some of the elements can be identified, though sutures are extremely difficult to distinguish. What little of the sutural pattern that can be discerned is not identical on the two sides, but this may be because the palatal bones have not been broken at the same level on each side.

The most easily identified elements are the paired pterygoids, the posterior regions of which extend slightly inwards towards the mid-line. The roots of small palatal teeth can be seen on the medial portion of the pterygoids. The ventral side of the right pterygoid was exposed by preparation, and the palatal teeth were found to be blunt and about 0·4 mm. in diameter.

The ectopterygoids also are clearly visible, lying postero-laterally to the pterygoids and forming the transverse flanges of the palate. Further forwards there is a large
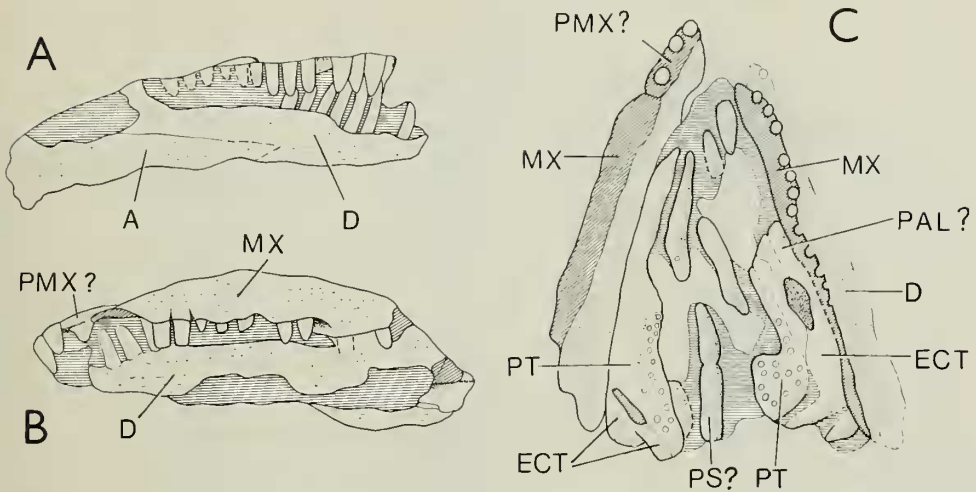
FIG. 1. *Eunotosaurus africanus*. BM(NH) no. 49424 (specimen E). Skull fragment × 3 (approx.). A, right lateral view. B, left lateral view. C, view of eroded dorsal surface of palate. Abbreviations: A, angular; D, dentary; ECT, ectopterygoid; MX, maxilla; PAL?, palatine?; PMX?, premaxilla?; PS?, parasphenoid?; PT, pterygoid. Horizontal lines indicate matrix; diagonal lines indicate broken surfaces.

foramen on the right side. Apparently bounded by the pterygoid, ectopterygoid and palatine, this is presumably the posterior palatal (or suborbital) foramen. It cannot be seen on the left side, but the bones of this region appear to have been folded, so that the area is covered by bone which originally lay more laterally.

An elongate fragment of bone lying in the midline between the pterygoids is probably part of the parasphenoid. Other pieces of bone lie more anteriorly, but these are too fragmentary and too disorderly in arrangement to provide any anatomical information.

VERTEBRAL COLUMN. Portions of the vertebral column are preserved in all eleven specimens. These portions vary in extent, from a series of ten articulated vertebrae to a few damaged fragments.

Size of specimens. Vertebrae and ribs are the only elements preserved in every specimen; since the ribs are often badly eroded, measurements of the vertebrae provide the only evidence of the relative sizes of the different specimens. Where possible, these measurements are of the lengths of individual centra. In some cases only the neural arches, and not the centra, of the articulated vertebrae are exposed. In these cases (specimens B, E and G) an approximate measurement of the total length of the series of articulated neural arches is given, since this should not be very different from the sum of the lengths of the centra themselves. These measurements are given in Table 1.

The vertebrae of specimen C are the best preserved, and this specimen has therefore been used as the standard for comparison in the following attempt to establish the relative sizes of the remaining specimens.

TABLE I

Lengths of vertebrae, in centimetres
(I indicates that the vertebra is preserved but incomplete)

Specimen	C (centra)	A (centra)	H (centra)	B (neural arches)	G (neural arches)	E (neural arches)
Dorsal 1	I				I	
2	0·8			I		
3	1·0	I				
4	1·1	0·95	I			
5	1·2	1·0	I	*c.* 5·4	*c.* 5·1	*c.* 4·2
6	1·2	1·0	I			
7	1·3	I	1·2			
8	1·15	I	1·0		I	
9	1·05	I	0·9	I		
10	I	I	0·8			
Sacral 1			0·75			
Caudal 1			0·7			
2			I			

The only vertebral measurement available in specimen F is the length of the fourth dorsal vertebra, from the anterior end of its prezygapophysis to the posterior end of the neural spine. This is 1·25 cm., indicating that the specimen is slightly larger than specimen C in which this distance is 1·1 cm. The neural arches of vertebrae 3 and 4 of specimen J are slightly (0·05 cm.) longer than those of specimen C. The centrum of the fifth preserved vertebra of specimen K is 1·4 cm. long, appreciably longer than any of the centra of specimen C. The vertebrae of specimen I are badly damaged, but direct comparisons show that they are slightly smaller than those of specimen C, but slightly larger than those of specimen H. Specimen D is too badly preserved for any measurements to be possible.

Specimens K and F therefore appear to be the largest. They are followed by specimens J, C, I, H and A in that order, all of which are of comparable size. These are followed by the noticeably smaller specimens B, G and E in that order.

Morphology of the vertebrae. As can be seen from Table 1, specimens C and H together provide a series of ten dorsal, one sacral and two caudal vertebrae. Many of these are also represented in other specimens, while cervicals and more posterior caudals are known from specimens J and K.

Specimen C contains the longest series of well preserved vertebrae (Fig. 2). As in all the other specimens, weathering has removed the neural spines of all those vertebrae which are preserved in their natural position. Fortunately, vertebra C8 had been displaced to a more ventral position, and its neural spine is perfectly preserved (Fig. 3). The anterior border of the neural spine slopes upwards rather gradually, but its posterior border is steeper. The spine is quite low but wide in proportion. The top of the neural spine lies posterior to a point halfway along the vertebra. There is no trace of a suture between the neural arch and the centrum.

The centra are notochordal and their ends are deeply concave. As can be seen from Table 1, their lengths steadily increase to a maximum at C7 and then diminish.
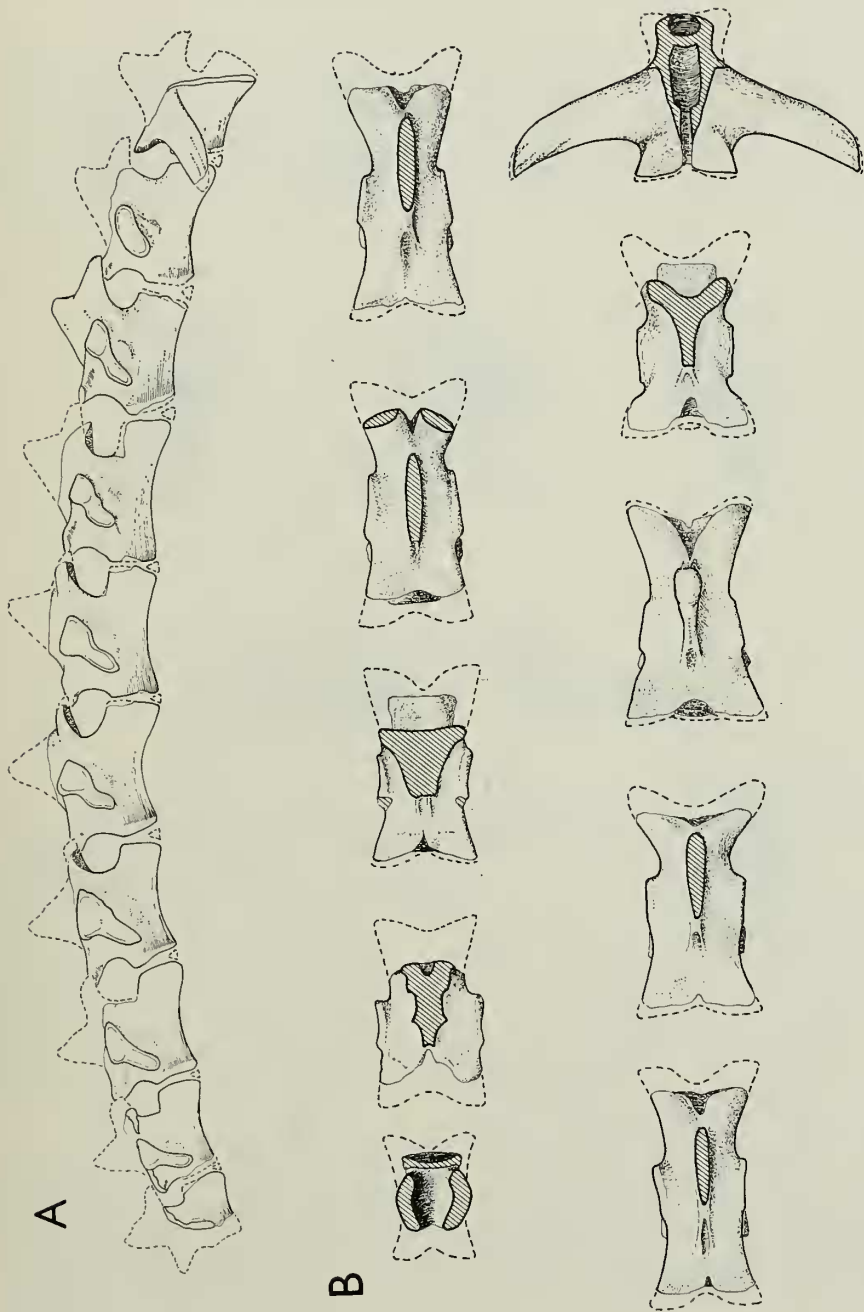
Fig. 2. *Eunotosaurus africanus*. BM(NH) no. R4949 (specimen C). Associated dorsal vertebrae 1–10. A, lateral view × 1·5. B, dorsal views, ×2.

The sides of the centra are slightly hollowed, so that the centra are rather hour-glass shaped in ventral view.

Tiny intercentra are visible in the ventral midline of specimen H (the natural mould), between the centra of the eighth, ninth and tenth dorsal vertebrae, and between those of the sacral and the first caudal. These areas are not exposed in the more anterior region of this specimen, but it seems reasonable to assume that they were present throughout the vertebral series. They were not detected during development of the other specimens, doubtless because of their small size and fragile nature.
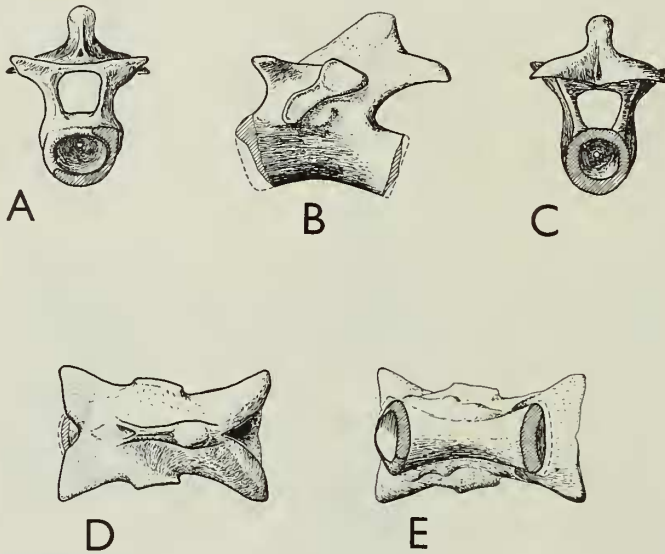

Fig. 3. *Eunotosaurus africanus*. BM(NH) no. R4949 (specimen C). Eighth dorsal vertebra, ×2. A, anterior view; B, lateral view; C, posterior view; D, dorsal view; E, ventral view

Cervical vertebrae. No cervical vertebrae are preserved as part of an associated vertebral column, but specimen K38 appears to be a cervical vertebra (Fig. 4A–D). This is indicated by its shortness compared with the elongated dorsal vertebrae, and by the fact that the rib facet is borne on a short transverse process. The neural spine is rather wide in anterior and posterior views, but pointed in lateral view. Vertebra I24, preserved under the anterior end of the series of dorsal vertebrae of specimen I. is closely similar to specimen K38.

Dorsal vertebrae. The zygapophyses are quite wide, and the post-zygapophyses are strengthened by being slightly swollen. The zygapophysial facets are horizontal, or nearly so, in all the vertebrae of specimen C. Though those of some individual vertebrae from other specimens (e.g. K40, Fig. 4E–H) are placed at a smaller angle to one another, it seems clear that the pose of the zygapophyses of specimen C is natural rather than the result of dorso-ventral compression. This follows from the fact that this horizontal pose is found even in the displaced vertebra C8. Since this was lying
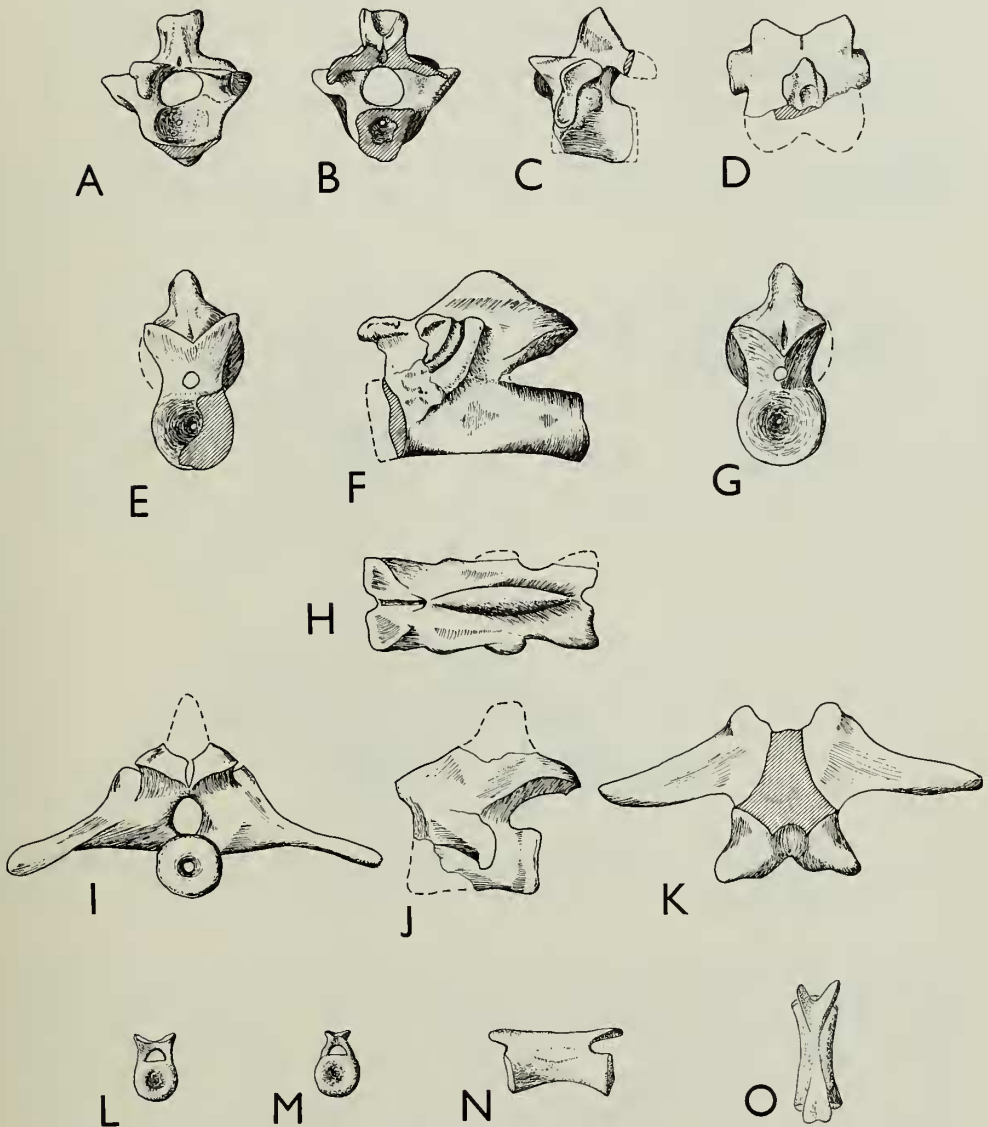
FIG. 4.   *Eunotosaurus africanus*.   USNM no. 23099 (specimen K) and BPI no. 3514 (specimen I).   Vertebrae, × 2.   A–D, specimen K38, cervical vertebra.   E–H, specimen K40, dorsal vertebra.   I–K, specimen K31, presumed anterior caudal vertebra.   L–O, specimen I24, posterior caudal vertebra.   A, E, L, anterior views; B, G, I, M, posterior views; C, F, J, N, lateral views; D, H, K, O, dorsal views.

on its side, any dorso-ventral compression of the specimen as a whole would have resulted in lateral compression of the zygapophyses of this vertebra.

There are no transverse processes on dorsal vertebrae 1–9, the ribs attaching directly to the neural arches. The facet for the rib lies on the anterior half of the side of the neural arch, sloping downwards and forwards; it hardly rises above the level of the zygapophysis. There is a low tubercle on the side of the centrum just posterior to the rib facet.

Three examples of the tenth dorsal vertebra are known: C10 (Fig. 2), H10 (Fig. 6) and K37 (Fig. 5). Unlike the other dorsal vertebrae, the tenth bears a large lateral
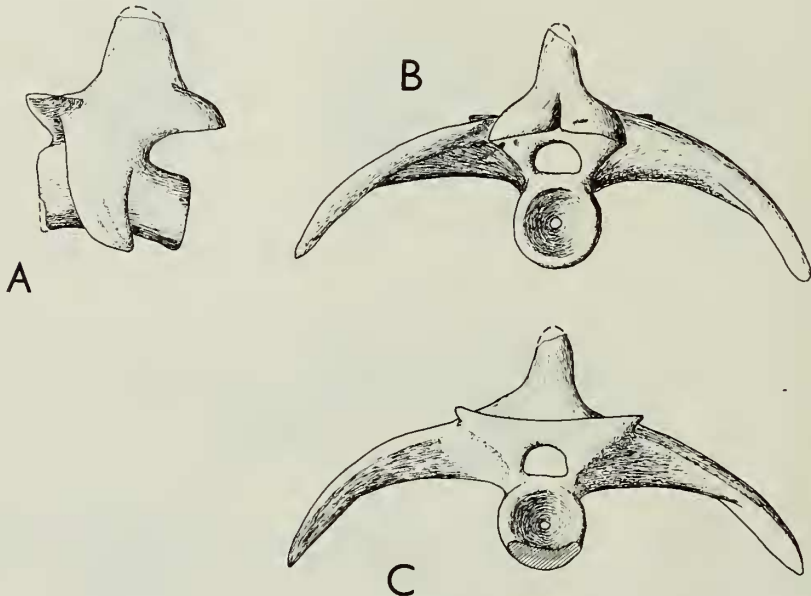

Fig. 5. *Eunotosaurus africanus*. USNM no. 23099 (specimen K). Specimen K37, last dorsal vertebra, ×2. A, lateral view; B, posterior view; C, anterior view.

process on either side; this arises from the side of the neural arch and curves ventro-laterally, tapering to a blunt distal end. That of specimens C10 and H10 curves slightly forwards, but that of K37 curves slightly backwards (Fig. 5). The dorsal surface of this process bears a pattern of longitudinal grooves similar to that found on the ribs of the more anterior dorsal vertebrae (Fig. 8). There is no trace of a suture between the neural arch and this process, which may therefore be either a transverse process or a co-ossified rib. The zygapophyses of this tenth dorsal vertebra are rather wide.

Sacral vertebra (Fig. 6). Specimen H (the natural mould) contains the only example of a sacral vertebra, which is preserved as part of an articulated series of vertebrae extending as far posteriorly as the second caudal. Only the ventral regions of this vertebra are preserved in the mould, but this includes the whole of the sacral

facet. The facet covers the whole of the internal surface of the associated ilium, and it is therefore clear that there was only a single sacral vertebra. As in the case of the preceding tenth dorsal vertebra, there is no sign of a suture between the neural arch and the sacral process. It is possible, therefore, that the ilium attached directly to the transverse process, but it is perhaps more likely that the sacral rib had become completely co-ossified with the neural arch.

The sacral rib (or transverse process) curves ventro-laterally and anteriorly. Its distal end does not reach as far laterally as does that of the preceding tenth dorsal vertebra. The expanded distal end is approximately diamond-shaped in outline (Fig. 6B) and bears a pattern of grooves similar to those found on the medial surface of the ilium.

Caudal vertebrae. The ventral regions of the first caudal vertebra, and of part of the second, are preserved as a natural mould in specimen H (Fig. 6). The transverse process of the first caudal is fairly powerful; it extends laterally and slightly anteriorly, curving ventrally to a distal end which is slightly expanded antero-posteriorly. The transverse process of the second caudal vertebra is more slender and is directed laterally, but also curves slightly ventrally.

Specimen K31 (Fig. 4, I–K) is probably a more posterior caudal vertebra. The transverse processes extend laterally and taper distally. The centrum is rather small compared with the size of the neural arch.
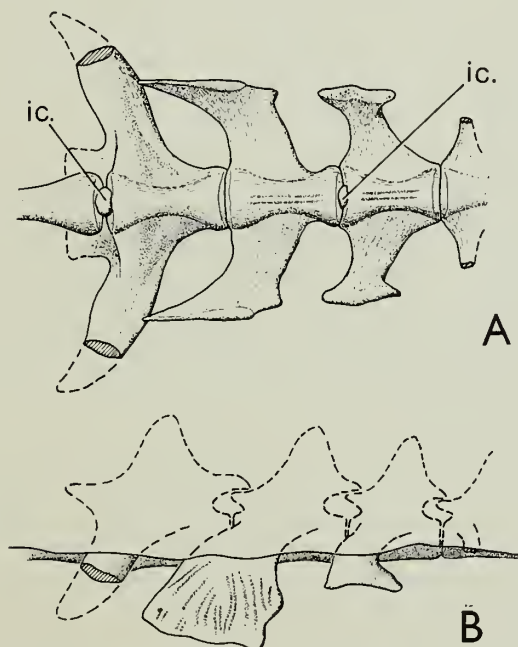

FIG. 6. *Eunotosaurus africanus.* SAM no. 4328 (specimen H). Cast of natural mould of sacral region, including ventral regions of last dorsal vertebra, sacral vertebra and first two caudal vertebrae, × 2. A, ventral view; B, lateral view. Abbreviation: IC, intercentrum.

Specimen I24 (Fig. 4, L–O) is an even more posterior caudal vertebra. It is an elongate centrally constricted cylinder, lacking any trace of a neural spine, with close-set zygapophyses.

RIBS (Figs. 7, 8).

TABLE 2

Specimen	A	B	C	D	E	F	G	H	J
Rib 1		✓	✓				✓		
2	✓	✓	✓			✓	✓		
3	✓	✓	✓	✓	✓	✓	✓		✓
4	✓	✓	✓	✓	✓	✓	✓	✓	✓
5	✓	✓	✓	✓	✓	✓	✓	✓	✓
6	✓	✓	✓	✓	✓	✓	✓	✓	✓
7	✓	✓	✓	✓	✓	✓	✓	✓	✓
8	✓	✓	✓		✓	✓	✓	✓	✓
9	✓	✓	✓		✓	✓	✓	✓	

Reconstruction. Ribs are preserved in all eleven specimens, though in many cases they are too incomplete to provide any useful information. Table 2 shows the number of ribs preserved in each specimen, except for specimens I and K. In each of these two specimens only five ribs are preserved, and those are so incomplete that it is impossible to determine where they belong in the dorsal series.

It was possible to remove completely from the matrix all the ribs of specimens A (eight pairs) and C (nine pairs). The following account is based on these specimens, unless otherwise stated.

In specimen C, the vertebrae (including the rib facets) and the proximal parts of the ribs (including the rib heads) are all well preserved and these elements could all be re-assembled. The more distal parts of the ribs are missing in this specimen, but are well preserved and almost undistorted in specimen A, in which the rib heads are missing. The shape of the rib cage had to be reconstructed using the information from both these specimens, since none of the eleven specimens included a complete series of undamaged ribs. Though there are obviously possible sources of error in this method, the resulting restoration (Fig. 7) provides a simple shape for the rib cage as a whole despite the complex shape of the individual ribs, and it seems likely that it is approximately correct.

The true edges of ribs shown in Fig. 7 are present in specimen A; the outlines of the more proximal regions of the ribs are restored from specimen F, in which these regions are well preserved. The ribs are more powerfully developed in specimen F (the largest specimen) than in specimens A and C, and the gaps between their expanded portions are smaller than those shown in Fig. 7. The vertebral column shown in Fig. 7A is that of specimen C, slightly reduced in size to approximate to that of the remains of the vertebral column of specimen A, and with the missing neural spines and parts of the neural arches restored (*cf.* Fig. 2B).

Morphology. The head of the first rib shows a slight trace of division into capitulum and tuberculum, but the remaining ribs are single-headed. This head

slopes strongly downwards and forwards (Fig. 7E). The proximal part of the rib also curves strongly upwards from the rib head (Fig. 7F).

As noted by both Seeley (1892) and Watson (1914), the most remarkable feature of *Eunotosaurus* is the way in which the outer surfaces of the dorsal ribs are expanded antero-posteriorly. These expansions together enclose the dorsal and dorso-lateral regions of the body almost completely. The remaining part of the rib is not expanded and runs like a rounded keel down the inner surface of the expanded area to its extreme distal end. Sections through the ribs show that this keel is hollow.

In all specimens where they are visible, the first and second ribs run backwards at a more acute angle than the remaining ribs. This is probably related to the presence of the shoulder girdle in this region (see below, p. 181).

The expansion of the first two ribs is confined to their proximal regions, that of the second rib being slightly larger than that of the first. The more distal part of the first rib is slender and rod-like, while that of the second is stouter and ends in a slightly concave oval facet.

The expansion of the first rib rises dorsally and only slightly posteriorly from its shaft. This fact is shown both by examination of the first ribs of specimen C, prepared free of the matrix, and also by the posture of the undisturbed first left rib of specimen G. Similarly, these specimens show that the expansion of the second rib lies considerably closer to the horizontal plane.

The degree of expansion of the more posterior ribs increases progressively to reach a maximum at rib 5, and then decreases progressively. The proximal parts of these expansions lie approximately in the horizontal plane, though those of the last two or three ribs may be inclined so that their surfaces face slightly postero-dorsally. As the more distal parts of the ribs curve round ventrally, the posterior border tends to flare outwards a little. This region may slightly overlap the front edge of the next rib, and it is worth noting that in all cases where the specimens show any overlap (e.g. specimen F) it is the anterior rib which overlaps the posterior.

The expansion of the third rib does not extend to its distal end; the distal portion of this rib is rod-like, ending in a concave facet like that of the second rib. The distal ends of the remaining ribs, 4–9, taper to a fairly sharp point. In ribs 4 and 5, in which the expansion is most fully developed, the posterior border curves rapidly forwards from the point of maximum expansion. The remaining ribs taper more gradually. Though the pointed ends of ribs 4–8 are slightly eroded in specimen A, casts of the natural mould (specimen H) confirm that these ribs lack the rod-like continuation and distal facet of ribs 2 and 3. The left ninth rib of specimen A is slightly larger than that of the right side.

Surface markings. A pattern of longitudinal ridges and grooves (Fig. 8) covers parts of ribs 2–9 (Fig. 7A, B). In general, these striations cover the distal parts of the expanded areas, but they are absent from the extreme distal regions of ribs 7 and 8.

PECTORAL GIRDLE (Fig. 9). No single specimen includes a complete pectoral girdle. The ventral, coracoid, region is present in specimens C, D and F; specimen D also includes a clavicle, a partial scapula and traces of the interclavicle. Part of the interclavicle is also preserved in specimen I.
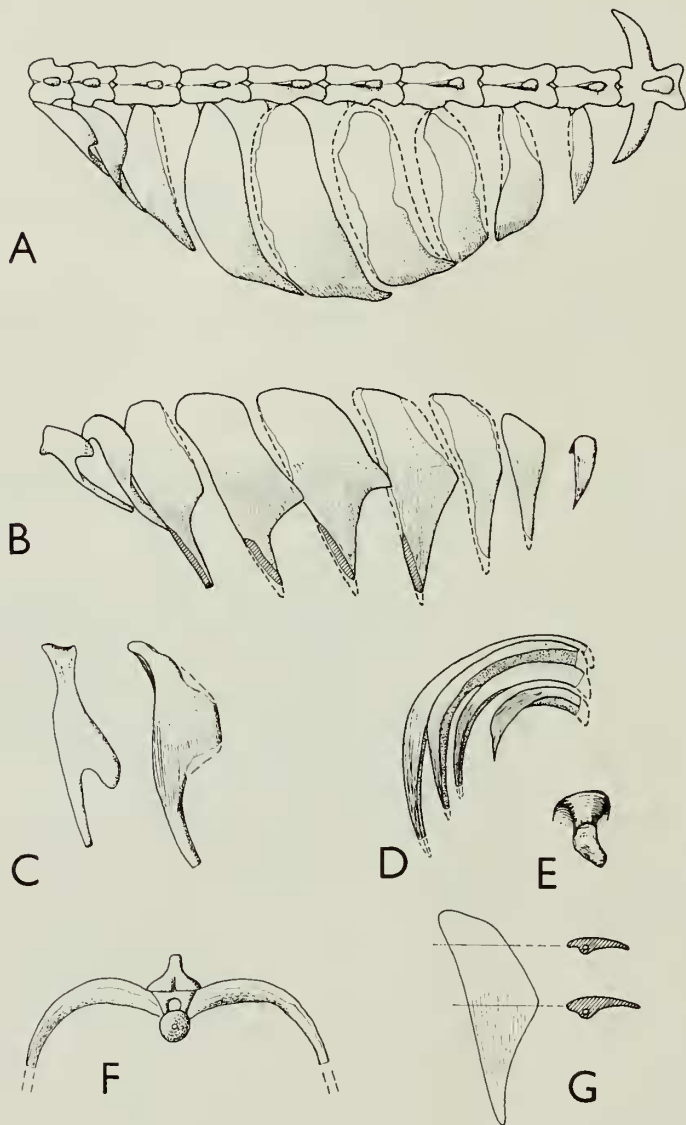
FIG. 7. *Eunotosaurus africanus*. Holotype, BM(NH) no. R1968 (specimen A), BM(NH.) no. R4949 (specimen C) and SAM no. K1132 (specimen F). Morphology of the ribs. A, B, rib cage reconstructed from specimens A, C and F (approx. natural size). A, dorsal view (including vertebral column); B, lateral view. C, ribs C1 and C2 in antero-dorsal view, natural size. D, posterior view of ribs A6–A9, natural size. E, medial view of head of left rib C5, natural size. F, specimen C, eighth dorsal vertebra and ribs in posterior view, natural size. G, rib C6, lateral view with cross-sections, natural size.

The dorsal, scapular, portion of the girdle lay in front of the first greatly expanded rib (the third) and lateral to the smaller first and second ribs.   This position is shown clearly in specimens C and F, and also by faint traces of the scapulae in specimens B and G.   The base of the scapula is preserved in specimens C, D and F, but the blade is present only on the right side of specimen D, and even this is damaged.   The preserved part of the blade is 1·8 cm. high, but its dorsal and anterior borders are missing; it is set at an angle to the midline of the body, the anterior edge being directed antero-medially (Fig. 13A).   It has a thickened posterior border and becomes thinner anteriorly.   There is no supraglenoid buttress or foramen, nor a suprascapular fossa. A groove on the inner side of the scapula leads ventro-medially into the dorsal opening of the coracoid foramen.
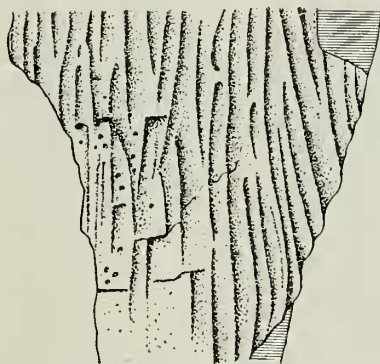

FIG. 8.   *Eunotosaurus africanus*.   Holotype, BM(NH) no. R1968 (specimen A).   Part of ornament of dorsal surface of distal region of rib A4, × 5.

The ventral surface of the coracoid region is eroded in all the specimens.   Its dorsal surface is well preserved in specimen C (Fig. 9A), but the different elements are so fused together that it is extremely difficult to distinguish any sutures.   The " grain " of the bone seems to indicate that the line of meeting between the scapula and the coracoid region ran through the coracoid foramen towards the glenoid.   It is not possible to be sure whether there was a coracoid alone or whether there was also a precoracoid.   A very well developed process for the head of the triceps muscle rises dorsally from the edge of the coracoid plate, just behind the rear edge of the glenoid.

The glenoid fossa is rather elongate.   The anterior region, on the scapula, faces laterally and somewhat posteriorly.   The middle region, where the fossa is highest dorso-ventrally, faces laterally.   The posterior region curves round on to the base of the triceps process to face laterally and slightly anteriorly.

A slender bone, 1·6 cm. long, lay near the midline of specimen D, just in front of the coracoids; one end of the bone is set at a slight angle to the remainder (Fig. 9D).   In view of its length and curvature, this bone is most easily interpreted as the left clavicle, the angled end meeting the acromion region of the scapula while the remainder of the bone ran along the front edge of the coracoid.   A small fragment of

bone which lies under the front edge of the right scapula may represent part of the cleithrum.

The median shaft of the interclavicle is preserved as specimen I28; it is narrow and flattened (Fig. 9B).   This region is also preserved, though badly eroded, in specimen D, where it reaches to the level of the posterior end of the coracoids.   An impression
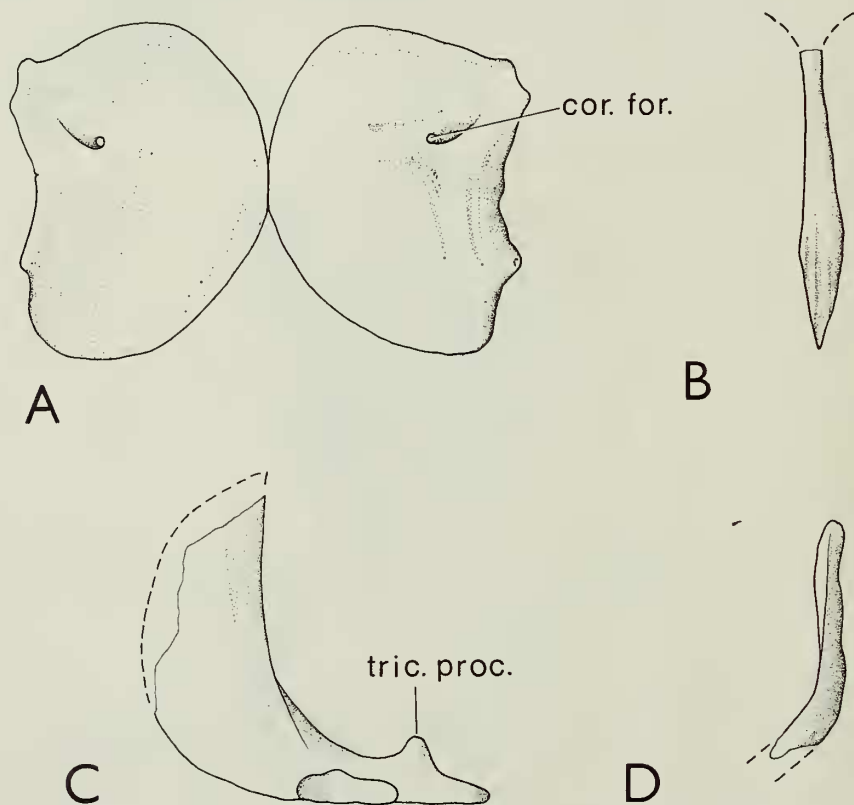

FIG. 9.   *Eunotosaurus africanus*.   BM(NH) no. R4949 (specimen C), BPI no. 3514 (specimen I), and BM(NH) no. 49423 (specimen D).   Pectoral girdle, ×2.   A, dorsal view of flattened ventral region of scapulo-coracoids of specimen C.   B, ventral view of interclavicle, specimen I28.   C, lateral view of scapulo-coracoid of specimen D.   D, anterior view of clavicle of specimen D.   Abbreviations: cor. for., coracoid foramen; tric. proc., process for head of triceps muscle.

of the anterior end of the shaft in specimen D shows that it became wider anteriorly, but the transverse region which met the clavicles is missing.

HUMERUS (Fig. 10).   Though several fragmentary proximal ends are preserved in specimens E, F and J, the only complete humerus is specimen K42, which is that of the right side.

The humerus, 3·5 cm. long, is rather slender in general appearance, the two expanded ends meeting at a narrow shaft region.   The planes of the two ends of the

bone are at an angle of about 50° to one another.   Although the exact pose of the humerus is uncertain, it will be described upon the assumption that the distal surface, which bears the capitellum, faced ventrally.

The head of the humerus is not very well developed.   It does not project on to the posterior surface of the proximal part of the humerus as a swollen area, but the anterior surface of this part of the humerus is slightly damaged.
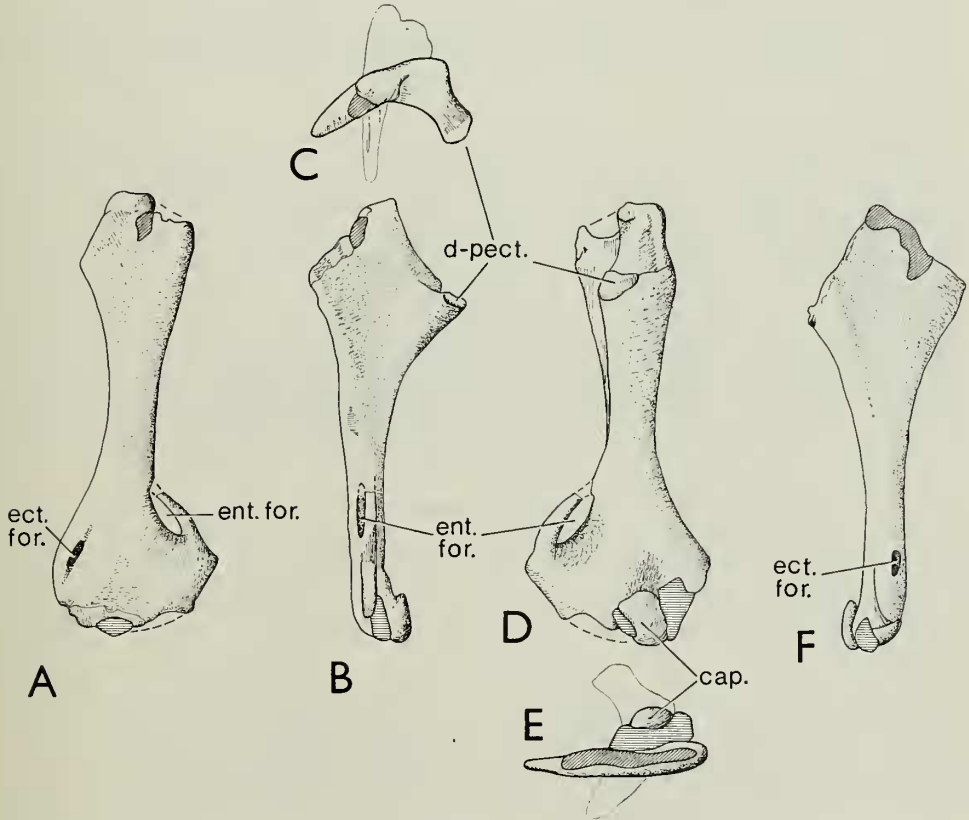

Fig. 10. *Eunotosaurus africanus.* USNM no. 23099 (specimen K). Left humerus, specimen K42, ×2. A, dorsal view; B, posterior view; C, proximal view; D, ventral view; E, distal view; F, anterior view.   Abbreviations: cap, capitellum; d-pect., delto-pectoral crest; ect.for., ectepicondylar foramen; ent.for., entepicondylar foramen.

The proximal half of the humerus consists of a rather flat, anteriorly-facing surface and a concave posteriorly-facing surface.   The latter is bordered ventrally by the prominent, powerful delto-pectoral crest, which is directed postero-ventrally.

The distal end of the humerus is rather thin.   Two openings can be seen on the almost flat dorsal surface.   A fairly large entepicondylar foramen pierces the bone close to its posterior margin; it runs distally and ventrally to open into a large concave

area on its ventral surface.   A much smaller ectepicondylar foramen pierces the bone close to its anterior margin; it runs distally and only slightly ventrally to open ventrally near the antero-distal corner of the humerus.   In addition to these foramina, the ventral view of the bone shows the well developed capitellum for articulation with the radius.   The region where the trochlear facet for the ulna would have been is unfortunately damaged.

No remains of the radius or ulna are preserved.   A few isolated and damaged podial elements are visible in specimen C.

PELVIC GIRDLE (Fig. 11).   The general morphology of the pelvic girdle is best shown by a cast of the natural mould of the almost complete right half of the pelvic girdle of specimen H.

The acetabulum is bounded anteriorly by a thick ridge on the ilium, but has no well defined posterior margin; it is therefore directed laterally and somewhat posteriorly. The ilium is quite narrow above the acetabulum.   The blade is directed dorsally and slightly posteriorly; its distal end is only slightly expanded antero-posteriorly, being no wider than the single sacral facet.   Both the lateral and the medial surfaces of the distal end of the blade both bear a pattern of ridges.

The edges and ventral surfaces of the pubis and ischium are damaged.   These bones meet the ilium at an angle of *c.* 105°.   The pubis and ischium also meet each other at a slight angle, so that the ventral surface of the ischio-pubic plate is slightly concave, The front edge of the pubis is quite thin; its edge below the acetabulum is damaged. There may have been a little post-mortem movement between the ischio-pubic plate
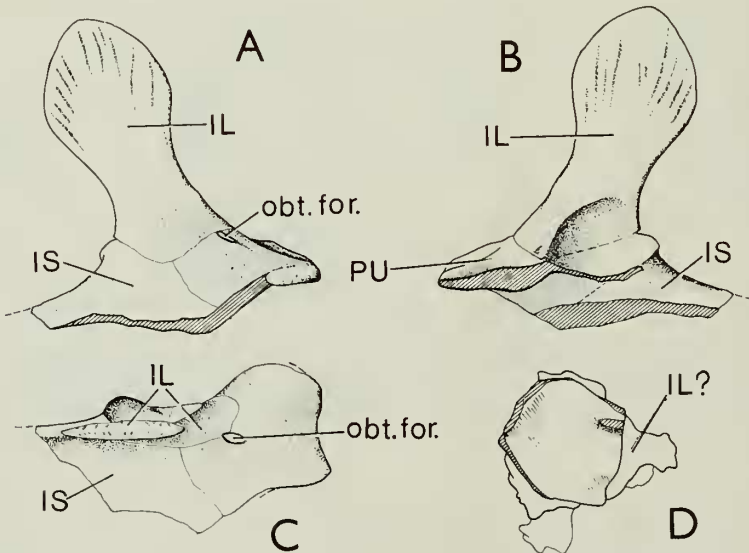

FIG. 11.   *Eunotosaurus africanus.*   SAM no. 4328 (specimen H).   Pelvic girdle, left side, × 2.   A–C, cast of natural mould of pelvis.   A, medial view; B, lateral view; C, dorsal view.   D, pubis (?) of holotype, BM(NH) no. R1968 (specimen A), × 2.   Abbreviations: IL, ilium; IS, ischium; obt.for., obturator foramen; PU, pubis.

and the ilium, since there is a slight notch between these two elements posterior to the acetabulum, and the ischium projects slightly into the acetabulum.

The obturator canal is well preserved in specimen K36, a left acetabular region, and runs dorso-ventrally. Though the position of the dorsal opening is not obvious at the corresponding position in specimen H, closer examination shows that there is a slight indication of its presence in the existence of a shallow elongate depression in the back edge of the pubis just medial to the level of the blade of the ilium. The foramen appears, therefore, to have been slightly occluded in specimen H, perhaps by the movement (mentioned above) between the ilium and the ischio-pubic plate. The ventral opening of the obturator canal lies immediately below its dorsal opening, within the pubis.

There is no trace of a thyroid fenestra in the preserved parts of the pubis and ischium. If the pelvis is placed against the sacral rib (which belongs to the same side of this same specimen), the preserved parts of the ischium extend to about one millimetre from the midline. The missing median regions of the pubis and ischium must therefore have been so small that it is impossible that they enclosed thyroid fenestrae.

A polygonal, notched element in the pelvic region of the holotype (Fig. 11D) was identified as a pubis by Seeley (1892). The pubis of specimen H is so incomplete that it is impossible to confirm this, but it remains a likely possibility. A pair of similar bones was found under the skull fragment of specimen E.

FEMUR (Fig. 12A–F). The only femur known is that from the right side of specimen A. The shaft is 2·0 cm. long and bears a number of ridges. Unfortunately, the relationships between these ridges and the features of the articular ends of the femur cannot be established, as the articular regions of this femur are lacking. This appears to be due, not to damage, but to immaturity, for the ends of the bone have the appearance characteristic of surfaces covered by cartilage: they are slightly concave and surrounded by a slightly projecting collar of periosteal bone. Even after making allowance for the absence of the articular portions, the femur seems surprisingly short compared to the humerus, which is 3·5 cm. long.

A strong ridge runs up the postero-dorsal corner of the proximal part of the bone. As a result of this ridge, there is an extensive posteriorly-facing surface on the femur. A lower ridge along the antero-ventral corner of the proximal part of the bone presumably led up to the internal trochanter. A depression which runs down the middle of the ventral surface of the distal part of the bone presumably continued into the popliteal space.

TIBIA AND FIBULA (Fig. 12G–K). The proximal ends of these two bones were preserved in specimen A, in articulation with the femur, but show no features worth description.

"DERMAL OSSIFICATIONS". Watson (1914) believed that traces of bone substance could be distinguished in specimen D, in two areas lying at a level above the ribs and neural arches, and believed that these were the remains of dermal ossifications. His figure (1914; plate VII, fig. 1) shows clearly the position of these two areas. They were closely examined before preparation of this specimen, and proved merely to be areas of discolouration, resulting from the detachment of fragments of matrix.
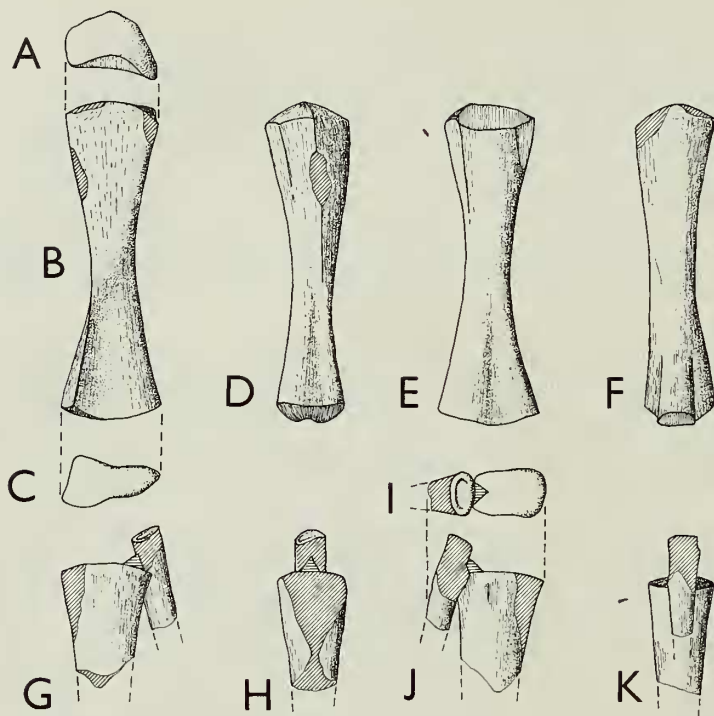
FIG. 12. *Eunotosaurus africanus.* Holotype, BM(NH) no. R1968 (specimen A). A–F, left femur, × 2. G–K, proximal regions of left tibia and fibula, × 2. A, I, proximal views; B, G, dorsal views; C, distal view; D, H, anterior views; E, J, ventral views; F, K, posterior views.

Despite careful observation, no sign of any bony elements was found during preparation of this specimen, nor in any of the other ten specimens.

III. RECONSTRUCTION AND FUNCTIONAL MORPHOLOGY

The vertebral column, ribs, girdles and humerus described above have been assembled together in Fig. 13. Most of these elements are derived from specimens A, C and H. These three specimens are all, as already noted, of the same order of size, and the error involved in assembling them together is therefore acceptably small. The humerus and the cervical and second caudal vertebrae shown belong to specimen K and are specimens K42, K38 and K31 respectively. From a comparison of the lengths of their last dorsal centra, it seems that specimen K is about 15 % longer than specimen H, and these bones have accordingly been reduced by 15 % from the original. The last vertebra shown in Fig. 13 is the isolated caudal I24.

The shortness, width and depth of the trunk region are very noticeable in Fig. 13. The carapace-like form which results from the expansion of the ribs could be
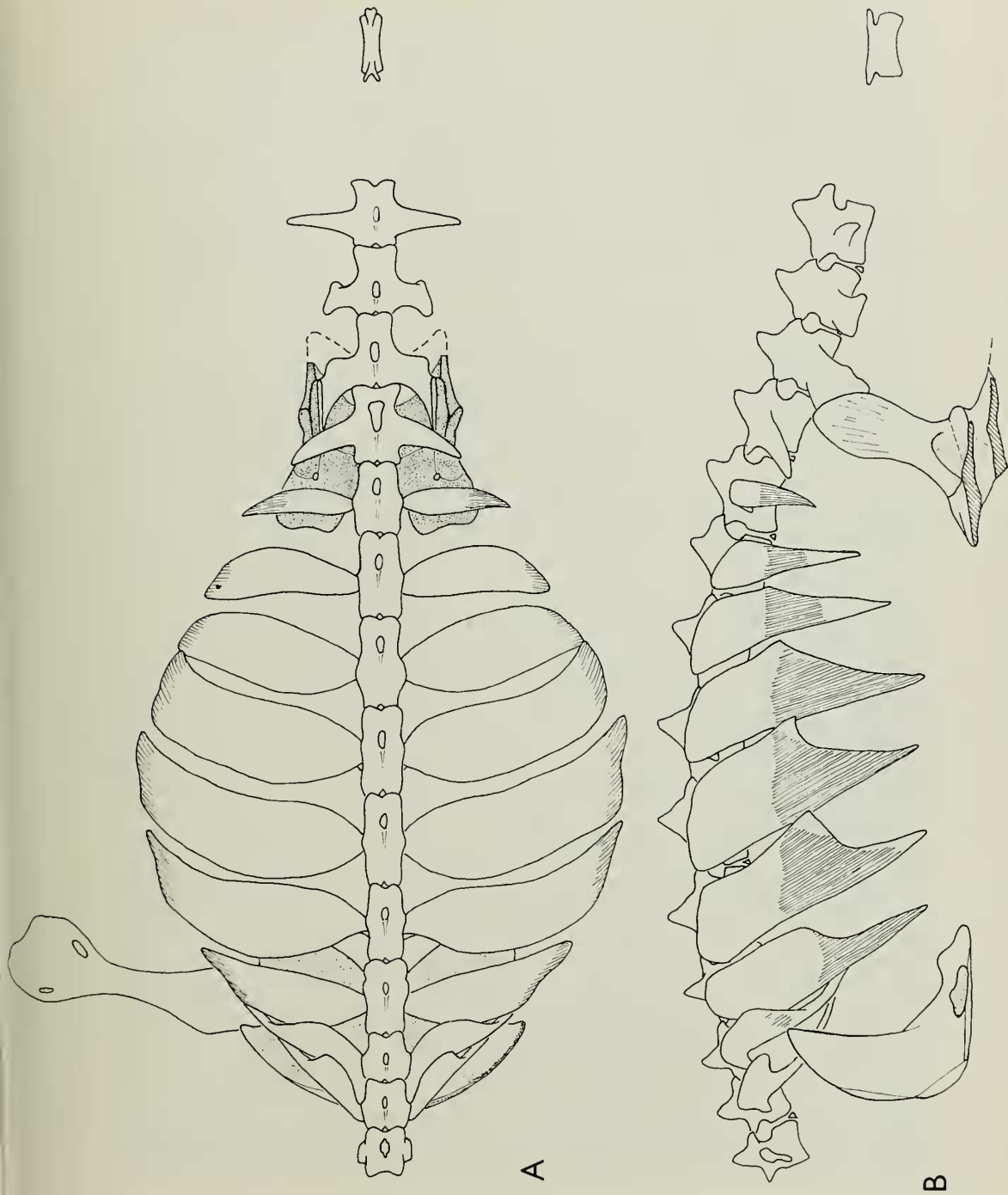
FIG. 13.   *Eunotosaurus africanus.*   Reconstruction of post-cranial skeleton, × *c.* 1·4.   A, dorsal view; B, lateral view.

interpreted either as a modification to carry dermal armour or as protective in its own right. In the first case, the degree of development of the ribs would imply the presence of a heavy and elaborate system of bony plates (*cf. Peltobatrachus*; Panchen, 1959). No traces of such an armour were found in any of the eleven specimens, even in specimens I, J and K, in which a number of dissociated bones were found lying under the rib cage. Furthermore, it would seem likely that the neural spines of the trunk vertebrae would have been enlarged distally to bear the median parts of such an armour (*cf. Stagonolepis*; Walker 1961) but they are not.

Since, then, it seems unlikely that the ribs were expanded to support a bony armour, their expansion presumably served in itself to protect the body. The presence of striations on the lateral parts of the ribs suggests that these areas must have been very close to the skin, and it is quite possible that they lay immediately underneath epidermal horny scales—the presence of such horny scales in all the living reptiles suggests that they originated early in reptile evolution.

If the striation of the lateral parts of the ribs implies that these areas were close to the skin, the lack of striation on their more dorso-medial parts similarly implies that there was here a greater thickness of other tissues, presumably muscular, between the ribs and the skin. This dorso-medial region of the ribs corresponds to the area which is normally occupied by the epaxial portion of the trunk musculature—the iliocostalis, longissimus dorsi and transverso-spinalis muscles. Other features of the ribs and vertebrae support the view that the trunk region still possessed at least a limited degree of flexibility and therefore retained the corresponding musculature. If there were no such flexibility, it would be expected that there would be some fusion between the expanded blades of the ribs, between the rib-heads and the vertebral centra, and between the vertebrae themselves. In fact, all these elements are distinct from one another, and there are well-developed zygapophyses between the vertebrae. These zygapophyses are horizontal, implying that the vertebral column was probably flexible only in the lateral plane. Some slight lateral flexure would have been permitted by two features. Firstly, each of the ribs slightly overlaps its posterior neighbour. Secondly, the simple nature of the single rib-head, and the orientation of this head on the vertebra, would have allowed the ribs on the contracted side to fold slightly inwards and postero-ventrally.

The vertebrae would have had to become elongate as the ribs widened, since the total length of the trunk centra must clearly be similar to the combined widths of the ribs. Such elongation of the vertebrae would in turn have resulted in an elongation of the body itself unless the number of trunk vertebrae had been reduced. This factor alone may have been responsible for the reduction in the number of trunk vertebrae, but its effects may have been aided by other factors. In most reptiles the length of the stride is increased by sigmoid flexure of the body, which in turn is facilitated by the presence of a large number of vertebrae, so that a few degrees of flexure at each intervertebral articulation will produce the sigmoid curve of the body. Once this flexibility had been greatly reduced by the expansion of the ribs, so that flexure of the body could no longer be used to increase the stride, the adaptive reason for retaining a large number of dorsal vertebrae would have disappeared. If the function of the expansion of the ribs was to provide protection for the body, it would then be

both possible and advantageous that the number of junctions between these ribs (effectively, chinks in the armour) should be reduced to a minimum.

It is interesting to note that a similar widening of the ribs is found in the living two-toed South American anteater *Cyclopes*.   However, nothing appears to be known about the functional significance of this feature.

The base of the tail of *Eunotosaurus*, as restored, appears rather powerful, but it should not be forgotten that the only anterior caudal vertebrae known are the first two (from specimen H) and one other isolated caudal (K31); it is therefore not possible to restore the rate of diminution of the tail with any degree of accuracy.   The long, tubular shape of the more posterior caudal vertebra (I24) suggests that the distal part of the tail was long and thin.

IV. THE RELATIONSHIPS OF *EUNOTOSAURUS*

Though very little of the skull remains, the presence of transverse flanges on the pterygoid bones is sufficient to answer the most fundamental question, as to whether *Eunotosaurus* is a reptile or an amphibian.   The presence of these flanges and of dorsal intercentra are reptilian features, absent in the microsaurs which in many ways parallel the early reptiles (Carroll & Baird 1968).

Since *Eunotosaurus* is found in the Middle Permian Tapinocephalus Zone, its possible earlier relatives must be sought among the Upper Carboniferous and Lower Permian reptiles.   These are known primarily from North America, with a few known also from European Russia.

In the absence of most of the skull, the relationships of *Eunotosaurus* must be deduced from the characteristics of its post-cranial skeleton.   The clearest indications of its probable position are provided by the structure of its vertebral column: relatively small, amphicoelous, notochordal centra; relatively large neural arches; more or less horizontal zygapophyses; small, low neural spines; persistent, though small, intercentra.   This type of vertebra, lightly built and providing little space for muscle insertion, is widespread in the small cotylosaurs—the captorhinomorphs and procolophonids.   Not surprisingly, the larger early reptiles such as the pareiasaurs and pelycosaurs have more strongly built vertebrae, with larger neural spines.   The absence in *Eunotosaurus* of the elaborate pareiasaur dentition also makes relationship to that group unlikely.   It is more difficult to exclude any possibility of relationship to the synapsids, because the modifications accompanying their large size would in any case mask any similarities to little *Eunotosaurus*.   However, this difference in size may in itself be a significant feature.   Even the smallest synapsid is four or five times the size of *Eunotosaurus*, and the synapsids are in general quite large reptiles, forming the fish-, flesh- and plant-eating elements of the Texas Lower Permian fauna. They, therefore, contrast greatly with the lizard-like captorhinomorphs which formed the invertebrate-eating element of this fauna (Olson 1966).   Little *Eunotosaurus* seems, then, more likely to be a specialized captorhinomorph than a survivor of an otherwise unknown, primitive type of synapsid.

Only a few of the small cotylosaurs, with which *Eunotosaurus* must now be closely compared, are sufficiently well known for a detailed comparison to be possible.   These are: *Hylonomus* (Carroll 1964) from the Lower Pennsylvanian Joggins Formation

of Nova Scotia; *Captorhinus* (Fox & Beerbower 1966) and *Araeoscelis* (Vaughn 1955), both from the Lower Permian Red Beds of Texas; and the early procolophonid *Nycteroleter* (Efremov 1940) from the Middle Permian Zone II of Archangel Province, U.S.S.R.   (*Araeoscelis* has been considered as a possible theropsid on the basis of its middle ear (Vaughn 1955) and as possibly allied to the ichthyosaurs and plesiosaurs on the basis of its temporal opening (Romer 1967).   However, the features of its post-cranial skeleton are almost identical with those of other small captorhinomorphs, and it seems best to regard it as merely a captorhinomorph which had developed a small temporal opening in the skull.)

In addition to the vertebral characteristics already mentioned, the following features are found in *Eunotosaurus* and in all the cotylosaurs mentioned above: the interclavicle has a long stem, there is a coracoid foramen in the pectoral girdle, an entepicondylar foramen in the humerus, and an obturator foramen in the pelvis.   Furthermore, in all except *Nycteroleter* there is a prominent knob behind the glenoid for the origin of the coracoid head of the triceps muscle, and the blade of the ilium is rather narrow, not greatly expanded antero-posteriorly.   However, these features are all characteristic of primitive reptiles in general.   Their presence in *Eunotosaurus* merely confirms that it is basically a primitive reptile, and that its closest relatives are therefore likely to be the cotylosaurs.

As might be expected from its early date, *Hylonomus* is structurally a possible ancestor for *Eunotosaurus*, as it is for all the other later cotylosaurs (for example, like *Eunotosaurus*, it has only a single sacral rib).   *Eunotosaurus* is therefore no less (and no more) closely related to it than are the other cotylosaurs.

None of the earlier cotylosaurs, of course, shows any positive signs of direct relationship to *Eunotosaurus* in having indications of reduction of the number of dorsal vertebrae or widening of the ribs.   It is possible to find individual characteristics in which *Eunotosaurus* is similar to one or other of these cotylosaurs, but in each case there are also other features in which the earlier form is more specialized than *Eunotosaurus* and therefore cannot be ancestral to it.   For example, the incomplete premaxilla of *Eunotosaurus* is slightly downturned upon the maxilla; this may be a post-mortem feature, but it is significant that the premaxilla of the captorhinids and of *Romeria* is downturned in just this way.   On the other hand, *Captorhinus* and its relatives in the family Captorhinidae (Seltin 1959) are specialized in the multiplication of the tooth rows in the middle and posterior parts of the jaws; there is no sign of this condition in *Eunotosaurus*.   *Araeoscelis* is the only other cotylosaur which possesses an ectepicondylar foramen in the humerus, but in its elongate lizard-like body it is quite unlike short-bodied *Eunotosaurus*.   In its lack of a supraglenoid buttress and foramen *Nycteroleter* is similar to *Eunotosaurus*; on the other hand, *Nycteroleter* is approximately contemporary with *Eunotosaurus* but already has three sacral ribs.

In conclusion it is clear that, on the one hand, *Eunotosaurus* is a cotylosaur and that, on the other hand, it is an extremely specialized genus, not closely related to any of the other known Permian forms.   Its position is best expressed taxonomically by transferring the family Eunotosauridae Nopcsa 1923 to the suborder Captorhinomorpha of the order Cotylosauria.

Eunotosaurus and the Chelonia.   The similarity between *Eunotosaurus* and the

Chelonia was noted by Seeley in his original description (1892), while Watson (1914), accepting and expanding this view, concluded that *Eunotosaurus* was possibly an actual ancestor of the Chelonia. As will be seen, the supposed features which led Watson to this opinion have now been found either incorrect or unreliable. It may therefore be as well to state at the outset of this discussion that there are no detailed similarities between *Eunotosaurus* and the Chelonia which would unequivocally and convincingly demonstrate a phyletic relationship between them. Therefore, if there were any relationship between the two, its possibility could be demonstrated only by showing that the features of *Eunotosaurus* were consistent with such a relationship, and by showing that the features of the Chelonia were comprehensible only if the group had passed through a *Eunotosaurus*-like stage in its history. These two aspects of the problem will be dealt with in turn.

As already mentioned, the skull fragment of *Eunotosaurus* shows few significant features. It now lacks the whole of the anterior end of the snout. However, Watson (1914, p. 1017) states " When I first saw the specimen the whole of the extreme anterior end of the skull was covered by matrix, which I removed with a needle under a Zeiss binocular dissecting microscope. Whilst doing so I found no trace whatever of any internarial processes of the premaxillae, and believe them to have been certainly absent; the anterior nares are consequently confluent and look directly forward ". As Parsons & Williams (1961) have pointed out, the external nares are not confluent in the earliest known indisputable chelonian, *Proganochelys* (= *Triassochelys*) from the Upper Triassic of Germany (Jaekel 1916). If Watson's interpretation were correct, *Eunotosaurus*, though earlier in time, would already be further advanced in this feature than *Proganochelys*. However, there seem to be some grounds for doubting Watson's interpretation. He stated that there were about eight maxillary teeth and three premaxillary teeth. In the present investigation, traces of nine left and twelve right maxillary teeth have been found, and Watson's identification of three pre-maxillary teeth has been provisionally supported. These facts indicate that all of the skull as described by Watson is still present, i.e. none of the snout has been lost during the intervening period. The orientation of this region, as seen in Fig. 1, certainly does not suggest that it includes the most anterior, median, portions of the complete premaxillae. It therefore seems likely that this part of the snout was lost before Watson prepared the specimen, that his dissection of the anterior region merely penetrated between the remaining fragments of the premaxillae, and that the morphology of the external nares is quite unknown.

Marginal teeth and tiny palatal teeth are present in *Eunotosaurus*, but these would be expected in any early ancestor of the Chelonia.

Watson (1914) also suggested that *Eunotosaurus* might have resembled the Chelonia in having a long, flexible neck. However, since his sole evidence for this was the fact that the only skull known was found lying under the body, his suggestion must remain completely hypothetical.

The main resemblances of *Eunotosaurus* to the Chelonia lie, of course, in the structure of the vertebrae and ribs of the trunk region. Watson believed that its vertebrae were Chelonia-like in that the rib attachments and neural arches lay very far forwards on the centra. However, the positions of the rib-facets and neural

arches of *Eunotosaurus* do not in fact appear to be at all unusual.   Since, as discussed above, *Eunotosaurus* also lacks the dermal ossifications which Watson believed he had detected, its chelonian features are restricted to those first noted by Seeley (1892): the trunk vertebrae are individually very elongate, but are reduced in number; they lack transverse processes, so that the single-headed ribs attach directly to the sides of the centra; and the expanded ribs resemble the chelonian carapace.

As has already been noted, the elongation of the vertebrae of *Eunotosaurus* is a result of the widening of the ribs.   Whether or not this similarity to the vertebrae of the Chelonia, and the resemblance of the expanded ribs to a carapace, indicate affinity must depend on one's view of the history of the chelonian carapace, and will be discussed below.

One very striking coincidence is the fact that in both *Eunotosaurus* and the Chelonia the number of trunk vertebrae has been greatly reduced, only ten or eleven remaining. The similarities and differences between the trunk and sacral regions of the two are best shown in the form of a table (Table 3), comparing those regions in *Eunotosaurus* and *Proganochelys*.   The ten dorsal vertebrae known in *Eunotosaurus* are compared to dorsals 2–11 (i.e., the last ten) of *Proganochelys*.

TABLE 3

Proganochelys		*Eunotosaurus*
Dorsal 1	Rib short and free	Not preserved
2	Rib joined to carapace for only part of its length	Rib slightly expanded
3	Rib incorporated into carapace	Rib slightly more expanded
4–10	Ribs incorporated into carapace	Ribs greatly expanded
11	Rib incorporated into carapace	Vertebra bears long, fairly wide fused process which may represent transverse process and/or rib
Sacral 1	Separate sacral rib	Sacral rib absent or fused to vertebra
2?	Rib unknown	1st caudal, but some expansion of distal end of rib/transverse process

There are, as can be seen, differences between the two forms.   Firstly, though only ten associated presacrals are known in *Eunotosaurus*, it is unknown whether any of the more anterior vertebrae were also dorsals.   If not, the trunk region of *Eunotosaurus* comprised only ten vertebrae, even fewer than in that of *Proganochelys*.   Secondly, the ribs of the last presacral and of the sacral in *Eunotosaurus* are not free but are either absent or (more likely) fused to their vertebrae.   Finally, there is only a single sacral vertebra in *Eunotosaurus*.   However, though there are two sacral ribs in some living Chelonia, there is no evidence of attachment of a second sacral rib to the ilium in *Proganochelys*.   The fact that the rear face of the first sacral vertebra of *Progano-chelys* is roughened suggested to Jaekel (1916) that the succeeding vertebra might have been suturally united with it, and the distal end of the first sacral rib bears a slight posterior facet to which a second sacral rib might have been attached.   Jaekel's view remains, however, a possibility rather than an established fact.

The lack of transverse processes on the dorsal vertebrae of both *Eunotosaurus* and the Chelonia, noted by Seeley, may merely reflect the facts that the flexibility of the column had been reduced or lost, and that the bony processes giving attachment to muscles producing this movement were correspondingly reduced and lost altogether. This similarity could, then, be due either to phyletic relationship or to convergence.

Turning now to the differences between the trunk vertebrae of *Eunotosaurus* and those of the Chelonia there is the fact, already noted, that the neural arches and ribs of *Eunotosaurus* are in their normal positions, above and lateral to the centra respectively. In chelonians, on the other hand, the neural arches lie intercentrally. This is probably due to their association with the neural plates of the carapace—it is clearly advantageous that these plates should cover the more vulnerable junctions between the centra rather than lie above the centra themselves. There seems, on the other hand, to be no obvious explanation of the intercentral position of the rib heads in chelonians.

Parsons & Williams (1961) believe that the width of the ribs of *Eunotosaurus* is a feature which rules it out as a possible relative of the Chelonia. They point out (p. 96) that " in several lines of marine turtles, the dermal component of the carapace is strongly reduced and the ribs appear as separate, narrow, well-spaced elements ". However, since these chelonians have strongly reduced the dermal component of the carapace, it would be surprising if they had retained broad heavy ribs, even if this were their original, primitive condition. Furthermore, though the ribs of these forms are not as expanded as those of *Eunotosaurus*, they are nevertheless slightly expanded and leaf-shaped rather than parallel-sided (*cf. Dermochelys* and *Protosphargis*, Zangerl 1939, figs. 1, 9).

There are many differences between the pectoral girdle of *Eunotosaurus* and that of chelonians, but these all result from the great specialization of this region in the Chelonia. In the absence of an external carapace, the pectoral girdle of *Eunotosaurus* remains lateral to the ribs, the coracoid is large, the glenoid is directed postero-laterally rather than antero-laterally, and the humerus is not strongly bowed. Similarly, in the absence of a plastron, the clavicles and interclavicle remain as small elements associated with the scapulo-coracoid. These differences are therefore to be expected.

Like the pectoral girdle, the pelvic girdle of *Eunotosaurus* is merely more primitive than that of the Chelonia. There is no evidence in *Eunotosaurus* of the large thyroid fenestra of living chelonians, but this is normally absent in primitive reptiles.

From the above discussion, it can be seen that nearly all the differences between *Eunotosaurus* and the Chelonia are due simply to the more primitive condition of *Eunotosaurus*. The absence of a free rib on the last presacral vertebra of *Eunotosaurus* may debar it from direct ancestry of the Chelonia.

As already mentioned, the significance of the similarities between the Chelonia and *Eunotosaurus* in the reduction of the number of trunk vertebrae, in the elongation of the vertebrae, and in the common possession of a protective development in the trunk region, must depend on one's view of the history of the chelonian carapace. Unfortunately, there is no palaeontological evidence on this question. *Proganochelys* of the Upper Triassic possessed a carapace which was already fully chelonian, differing

from the living forms in three points only.   The first dorsal vertebra of *Proganochelys* has become an additional, last, cervical in the later Chelonia; the ribs of the second dorsal vertebra of *Proganochelys* are joined to the carapace (though for only the middle part of their length), whereas the corresponding ribs in later chelonians are greatly reduced and do not touch the carapace; finally, the last presacral rib is incorporated into the carapace in *Proganochelys* but is small and free in later chelonians.   These points merely indicate what is in any case clear on other grounds, that the number of body segments involved in the trunk and carapace has been progressively reduced in the Chelonia.

It is possible to reconstruct a theoretical history of the chelonian carapace, beginning with a *Eunotosaurus*-like stage in which the ribs are enlarged and covered by horny epidermal plates.   If the dermis below these plates were to produce bony plates, as it does in many reptiles, these might eventually cohere to form a carapace, the contribution of the ribs to this structure being concurrently reduced.   However, since a protective bony armour was already in existence, there seems to be no obvious reason why the main rôle in the formation of this armour should be thus transferred to a new and more superficial level.   Furthermore, if the expanded ribs of *Eunotosaurus* represent a fairly advanced stage in the development of the carapace, it is somewhat surprising to find no sign of any corresponding advance towards the development of a plastron.

An alternative theory, excluding any *Eunotosaurus*-like stage, would be that the dermal armour arose first, as a series of segmental plates similar to those of the Triassic stagonolepidids (Walker 1961).   As suggested above in the discussion of *Eunotosaurus* itself, the development of an armour limiting the flexibility of the body would probably be accompanied by a reduction in the number of trunk segments. (Indeed, this process seems to have occurred also in the Triassic placodonts, in which unarmoured *Helveticosaurus* had *c.* 31 trunk vertebrae, while only fourteen remain in the most heavily armoured form, *Henodus*.)   The armour would originally have been separated from the ribs and vertebrae by the dorsal musculature of the body, but this would have been progressively reduced and lost as the flexibility of the trunk region was diminished.   The armour would at this final stage come into contact with the vertebrae and ribs.   As Ruckes (1929) has shown, the ribs are drawn into a superficial position, dorsal and lateral to the girdles, because they become incorporated into the developing carapace.   This is readily explicable if, as suggested here, the carapace was from the beginning general and superficial, and therefore itself lay lateral to the girdles.

Though by its nature inconclusive, one further line of reasoning seems to be worth discussing.   It is surprising, if *Eunotosaurus* is ancestral to the Chelonia, that no chelonian remains have been found in faunas of ages intermediate between the Mid-Permian Tapinocephalus Zone (which contains *Eunotosaurus*) and the Upper Triassic Stubensandstein and Knollenmergel of Germany (which contain the earliest indisputable chelonian, *Proganochelys*).   This lack cannot be ascribed to a poverty of vertebrate faunas of this period, or to a poverty of vertebrate faunas of any particular ecological nature.   The vertebrates of the period of time between *Eunotosaurus* and *Proganochelys* are preserved in the abundant terrestrial faunas of the Endothiodon,

Kistecephalus and Cynognathus Zones and the equally abundant semi-aquatic fauna of the Lystrosaurus Zone, all of South Africa, followed in Europe by the fresh-water Bunter fauna and the marine Muschelkalk fauna, in East Africa by the terrestrial Manda fauna, and in South America by the terrestrial Chañares, Santa Maria and Ischigualasto faunas. Equally, the lack of chelonian remains throughout this period cannot be ascribed to any inherent properties of these remains; they are not particularly difficult to identify, nor particularly fragile. Indeed, quite the reverse, for not only are the elements of the axial and appendicular skeleton highly recognizable, but the stout bony elements of the carapace and plastron provide additional and highly characteristic evidence of the presence of the group. These points make it seem somewhat unlikely that the chelonians had been in existence for very long before they are first found in the Upper Triassic, and therefore unlikely that they are descended from Mid-Permian *Eunotosaurus*.

It can be seen from the above discussions that neither the comparative morphology of *Eunotosaurus* and the Chelonia, nor the probable history of the chelonian carapace, nor the evidence of the fossil record, supports the view that *Eunotosaurus* was ancestral to the Chelonia.

V. ACKNOWLEDGEMENTS

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